



Review

Cite this article: Cowie RH, Bouchet P, Fontaine B. 2026 Devastation of island biodiversity: a land snail perspective. *Phil. Trans. R. Soc. B* **381**: 20240425.
<https://doi.org/10.1098/rstb.2024.0425>

Received: 24 June 2025

Accepted: 18 September 2025

One contribution of 18 to a theme issue 'The biosphere in the Anthropocene'.

Subject Areas:

ecology

Keywords:

extinction, biodiversity, conservation, biological control, *Euglandina*, habitat destruction, predation, *Platydemus*, oceanic islands, captive breeding

Author for correspondence:

Robert H Cowie

e-mail: cowie@hawaii.edu

Devastation of island biodiversity: a land snail perspective

Robert H Cowie¹, Philippe Bouchet² and Benoit Fontaine²

¹Pacific Biosciences Research Center, University of Hawaii, Honolulu, HI 96822, USA

²Muséum National d'Histoire Naturelle, Paris 75005, France

RHC, 0000-0002-2986-7092

Many islands are remote and the level of interest in land snails as a component of the global biodiversity conservation agenda is low. The conservation status of many island land snail faunas thus remains at best out of date. However, land snails have an asset that other groups do not—their shells, which can remain *post mortem* in the shell bank of the soil for many tens or several hundreds of years after the death of the animal. Consequently, numerous island land snails are known only based on empty shells—modern but of uncertain age, and thus escaping the strict requirements for Red Listing extinctions after AD 1500. Many high volcanic islands had extraordinarily diverse and highly endemic land snail faunas, with 50–100 endemic species on land masses sometimes as small as 30–50 km². 'Devastation' is not a hyperbolic term to describe the fate of many of these island microcosms, with levels of extinction variously documented but not uncommonly in the order of 30–50%, and up to 80%. Historically, loss of habitat—namely deforestation—has been the prime cause of species loss, triggered or accelerated by the introduction of livestock and other feral mammals, which did not directly impact the snails but contributed to habitat loss and degradation. Another wave of extinctions followed the introduction—mostly deliberate—of non-native carnivores (snails and worms), directly preying on endemic snails that had evolved in the absence of such predators. The most infamous of these failed 'biological control' plans was the introduction of neotropical predatory snails, *Euglandina* spp., to the high islands of the remote Pacific to control the giant African snail pest, *Lissachatina fulica*, resulting in the extermination of several tens—and probably hundreds—of narrow-range endemic land snail species. Ornamental use of shells and hobbyist shell collecting may have impacted populations of larger, more colourful species. By contrast, climate change has not been documented as having caused any land snail extinctions. Few land snails are charismatic animals and, in view of the broad and deep impact of aliens on devastated natural habitats, *in situ* conservation of endemic island snails appears to be possible in only rare cases. There are, however, limited initiatives for *ex situ* conservation that can buy time and offer a glimmer of hope for positive thinking. Concerted and targeted field work to find and collect representative specimens of remaining species is needed in order that knowledge of the existence of these diverse faunas be available to posterity.

This article is part of the theme issue 'The biosphere in the Anthropocene'.

1. Introduction

Islands come in many kinds and many sizes: oceanic islands that have never been connected to a continent and are either volcanic 'high' islands (e.g. Galapagos, Ogasawara, Iceland, Azores, Mauritius, St. Helena), some now only represented by atolls (e.g. Maldives), including raised limestone islands

(e.g. Makatea in French Polynesia, Henderson in the Pitcairn group, Rock Islands of Palau); or land-bridge islands that were connected to a continent prior to sea level rise (e.g. Great Britain, Tasmania); continental islands that became isolated as a result of continental drift or fragmentation (e.g. New Zealand, Madagascar, Seychelles) and may have been inundated by subsequent sea level rise (New Caledonia); and others that reflect complex series of vulcanism, uplift, sedimentation, plate movement and terrane accretion (e.g. Aegean Islands, Jamaica, New Guinea, Socotra, Sulawesi) (e.g. [1–5]). In addition to these marine islands, there are numerous islands within rivers and lakes, and ancient lakes can themselves be considered ‘islands’ surrounded and isolated as they are by terrestrial environments (e.g. [6]). Karst outcrops (e.g. in Southeast Asia) surrounded by more acidic soil substrates may be considered islands [7] and even mountain tops on continents may be referred to as ‘sky islands’ [8]. From a biological perspective, the biotas of all kinds of islands are similarly isolated, have evolved in isolation, thereby now consisting mostly of endemic species prior to anthropogenic introductions, and suffer equivalent threats leading to extinction of these isolated endemics.

Islands surrounded by sea constitute approximately 6.7% of the Earth’s land area, but sustain 20% of its species-level biodiversity, 50% of endangered species and 75% of known extinctions [5]. The temporal pattern of destruction of these island biotas is largely mirrored across the globe, though with different starting points and trajectories, primarily associated with human colonization of previously uninhabited islands [9]. Here, we focus primarily on oceanic islands, which have relied entirely on dispersal for the origins of their native biotas [10], but also touch on other marine islands. Discussing non-marine islands is beyond the scope of this contribution.

Oceanic islands and other marine islands support highly endemic and diverse biotas (e.g. [11–13]). But they have suffered extensive habitat destruction, especially deforestation, caused by agricultural and urban/suburban development and the impacts of invasive species, notably ungulates (pigs, sheep, goats, cattle), leading to decline and extinction of native plants and native animals as their habitat vanished [5,9]. Other invasive species have preyed on the native species, or perhaps out-competed them, some of these predators becoming widespread globally (e.g. [14]).

Oceanic island land snail faunas are among the most heavily impacted of any major group of plants or animals, with extremely high levels of extinction on some islands and in certain iconic groups of species, especially in the Pacific (e.g. [15–22]). However, many islands are remote, and the level of interest in land snails within the overall biodiversity conservation agenda is low. These two factors render the conservation status of many island land snail faunas, at best, out of date, based on surveys that are 20–100 years old. Nonetheless, land snails have an asset that other groups do not—their shells, which can remain *post mortem* in the shell bank of the soil for many tens or several hundreds of years after the death of the animal. In this respect, they parallel birds, the bones of which offer a window on now-vanished biodiversity [23]. Numerous island land snails are thus known only as empty shells—modern but of uncertain age, and thus escaping the strict requirements for Red Listing extinctions after AD 1500. Many oceanic high islands had extraordinarily diverse and highly endemic land snail faunas, with 50–100 endemic species on land masses sometimes as small as 30–50 km² (e.g. [20,24–28]). ‘Devastation’ is not a hyperbolic term describing the fate of many of these island microcosms, with levels of extinction variously documented but not uncommonly in the order of 30–50%, and up to 80% or more.

The IUCN [29] has evaluated the conservation status of 93 351 animal species, of which 789 (0.8%) are listed as Extinct and 18 109 (19%) are in the Threatened categories (Critically Endangered, Endangered, Vulnerable). At the time of writing, MolluscaBase listed 88 062 accepted mollusc species, of which 29 124 were terrestrial gastropods [30]. Of 9144 molluscs evaluated by the IUCN (10% of the total known species), 3662 are terrestrial gastropods, and of these, 184 (5.0%) are listed as Extinct and 1124 (31%) as Threatened. By contrast, of 13 442 insects evaluated (1.3% of known species), only 59 (0.4% of those evaluated) are listed as Extinct and 2565 (19%) as Threatened; of 11 195 birds evaluated (100% of known species), 164 (1.5%) are listed as Extinct and 1311 (12%) as Threatened; and of 6025 mammals evaluated (89% of known species), 85 (1.4% of those evaluated) are listed as Extinct and 1363 (23%) as Threatened. Thus, terrestrial gastropods (and other island groups) are suffering an especially high level of extinction as well as being one of the most highly threatened animal groups, a status that has been acknowledged for some time [20,31–33].

Moreover, many species are known by experts to be extinct, though not listed by the IUCN. Among molluscs, 638 species have been considered extinct, 380 possibly extinct and 14 extinct in the wild, a total of 1032 species (listed by Cowie *et al.* [34]), and more than twice as many as listed at that time by the IUCN in these categories (462). Approximately 70% of mollusc extinctions are of island species, almost exclusively land snails, with by far the greatest number from the Pacific [31,32]. Most of these island species were single island or single archipelago endemics and thus highly vulnerable to extinction based simply on their restricted ranges. And because of their isolation and evolutionary radiation on a multitude of small islands, these island extinctions constitute a major portion of global land snail species extinctions.

This contribution takes a global perspective on island land snail faunas, many of which are especially diverse, while focusing primarily on those of the Pacific, which have suffered the most drastic losses. It is likely that there have been extinctions of land snail species on many islands not mentioned here, but it is impossible to provide an exhaustive treatment of the issue within the constraints of a publication such as this. Instead, this review summarizes the most well-known and documented island land snail faunal extinctions, providing an overview of this significant loss of global biodiversity. Land snail nomenclature follows MolluscaBase [30].

2. Causes of extinction

Causes of extinction of land snails, as for most other groups, often fall into relatively clear categories, both non-anthropogenic and anthropogenic. The former includes Pleistocene climate change and sea level rise and fall, and geological events (e.g.

volcanic, plate tectonic). The latter includes, perhaps most importantly, habitat loss and the introduction of non-native species, but also exploitation, collecting and, to a minor degree, potential modern climate change.

(a) Non-anthropogenic causes

(i) Pleistocene and early Holocene climate change and sea-level fluctuations

So-called 'fossil' or 'subfossil' shells (the distinction variably defined in the literature, e.g. [35]) are well known from aeolianite (or eolianite) deposits, often referred to as lithified sand dunes, on islands. Formation of these dunes is a complex process, which may differ among locations, associated with patterns of deposition of wind-blown sand differentially during high and low sea-level stands of the Quaternary interglacial and glacial periods. Most of these systems are in warmer regions where the trade winds blow, and many are on islands [36]. Some of these dune systems have received considerable attention, notably those in the Hawaiian Islands (figure 1) [37,38] and Bermuda [39,40]. And some of these islands have well-documented radiations of land snails, many of them extinct and only found in Pleistocene lithified dunes.

Notably, of the 11 species of *Poecilozonites* known from Bermuda [30], only two remain extant, *P. bermudensis* and *P. circumfirmatus*, both listed in the IUCN Red List [29] as Critically Endangered. *Poecilozonites reinianus* was last reported alive by Peile in 1926 [41] but could not be found by Gould (1991; [42]) nor by Bieler & Slapcinsky (2000; [43]); the remainder are extinct, most of them known only as Pleistocene fossils [43,44].

The Hawaiian Islands, much larger than Bermuda and with a much more numerous land snail fauna [45], have extensive aeolianite deposits with a diverse representation of species, genera and families. Notable examples include the 21 recognized species in the extinct genus *Carelia* (Amastridae) [45,46], endemic to the islands of Kauai and Niihau, some of which occurred in inland forested areas and survived into the twentieth century, in one case (*C. bicolor*) last seen in 1970 [47]; others are only known from sandy coastal deposits and, based on the condition of their shells, were presumed to have been buried alive as the wind blew the sand over them [46,48]. Representative endemic species of other land snail groups are also found in Pleistocene dunes on Kauai alongside *Carelia* spp., including other amastrids (the family is endemic to the Hawaiian Islands), as well as heliciniids, endodontids, microcystids and vertiginids [49]. Similar communities of fossil land snails are also found in aeolianite deposits on the Hawaiian islands of Oahu [50] and Molokai [51]. Among the Hawaiian heliciniids (14 species [45]), Neal [52] reported six species known only as fossils and three known from both fossil and living specimens, with some of the fossil material specifically noted as from dunes. Many amastrids have been described as fossils or subfossils from Pleistocene deposits, found not only in dunes but also road and railway cuttings and house building sites, as well as from 'pockets' of Pleistocene deposits at higher elevations on these and other Hawaiian islands [48,50,53]. The Amastridae numbered 325 known, described species [45]. Late Pleistocene and early Holocene climate change associated with sea level fluctuations may have caused the extinction of most, if not all, of the 43 of them that were described as fossil or subfossil, some specifically from Pleistocene deposits, but more recent impacts, as described below, have led to the almost complete demise of this Hawaiian endemic family, with fewer than 10% of the species remaining [19].

Elsewhere in the Pacific, fossil *Mandarina* in the Ogasawara Islands exhibited periods of morphological and community stability interrupted by rapid morphological change, speciation and extinction, most notably associated with climate change corresponding to the period of lowest sea level and the end of the last glacial period [54].

In the Atlantic, palaeontological data on the land snails of Madeira from the Middle Pleistocene to just before the arrival of human colonizers suggest that climatic change altered the island's vegetation, which changed increasingly from grassland to woodland, and caused consequential changes in faunal composition and the distribution of species, with a significant number of species going extinct [55]. Somewhat similar patterns of faunal change, including extinctions, occurred on Porto Santo, also in the Madeiran archipelago, but were not attributable unequivocally to climate change [56]. Later extinctions on both islands, as well as on the Desertas Islands, were attributed by these authors to human activities (§2b(i)).

Finally, in Jamaica, local extinctions of species still extant elsewhere on the island have been attributed to late Pleistocene or early Holocene climate change [57]. Subsequent extinctions resulted from anthropogenic habitat destruction (§2b(i) below).

All the above instances of Pleistocene and early Holocene extinction took place prior to the arrival of humans on these islands.

(ii) Geological events

There are few Recent documented land snail extinctions for which anthropogenic impact is excluded, e.g. the land snail *Zonites santoriniensis*, endemic to Santorini in the Aegean Sea, which probably did not survive the cataclysmic eruption of the island in around 1500 BC [58]. Also, *Zonites siphnicus*, reported from the islands of Folegandros, Sicanos and Siphnos to the northwest of Santorini, is known only as a fossil but the cause of its extinction is unclear [59].

Many endemic Galapagos bulimulid land snail species may have faced natural hazards including volcanic eruptions and prolonged drought, leading to their extinction; but the decline to extinction may have been exacerbated by anthropogenic changes, if not entirely caused by them [60].

Regarding the Mascarene Islands, it has been suggested that little of the original biota may have survived the cataclysmic volcanic eruptions that occurred around 200 000 (Réunion) and 500 000 (Mauritius) years ago [1]. This suggestion was based on a citation of this as a possibility for the Réunion avifauna [61]; whether it could have been the case for the land snails is unknown. Similarly, the five known land snail species of Krakatau in Indonesia prior to the devastating volcanic explosion of



Figure 1. Lithified and eroded sand dunes, Laie Point and Kukuīhoolua Island, Oahu, Hawaiian Islands (photo: R.H. Cowie).

almost the entire island in 1883 have not been found on the remnants subsequently [62]. While these species were not endemic to Krakatau, all the land snails of the island, some of which may have been endemic, perished.

(b) Anthropogenic causes

(i) Habitat loss and indirect impacts of invasive species

On many islands throughout much of the world, but especially in the tropics and subtropics, habitat loss has been the earliest manifestation of human impact, often intertwined with the impacts of non-native invasive species [63]. Invasive species may drastically alter habitat, which may then facilitate the spread of other invasive species. These species may act in concert with or subsequent to habitat alteration, making it difficult, with some clear exceptions, to say whether invasive species, *per se*, have caused the extinction of a particular species [64].

In the Pacific, early human settlement of oceanic islands led to the clearing of low and middle elevation habitats, mostly forest, to make way for habitation and agriculture. Sometimes, invasive plants might themselves have been the cause of significant habitat modification, rendering the habitat unsuitable for the native fauna, while introduced animals, especially ungulates, have caused rapid and extensive destruction of forest.

The Hawaiian Islands supported at least 750 known native species of land snails (all but two to four of them endemic) [45]. Prior to the arrival of Europeans in 1778 (the English explorer Captain James Cook), native Polynesians developed extensive agricultural systems, both stream-fed irrigated wetland systems at low elevations and rain-fed terracing up to 900 m in elevation (figure 2), particularly on the largest and highest island, Hawaii island itself [65,66]. This led to the extinction of several land snail species [67]. Native lowland vegetation may also have been impacted by introduced Polynesian rats [68], and perhaps also domestic Polynesian pigs, possibly thereby rendering the habitat unsuitable for the resident endemic snails. However, with the arrival of Europeans and their introduction of ungulates that became feral [69], the scale of native habitat loss expanded [70]. Initially, cattle were the most destructive; huge feral herds derived from the four cows and two bulls that another English explorer, Captain George Vancouver, left on Hawaii island in 1793 eventually had to be brought under control and led to the development of major cattle ranching on that island especially [71]. But more persistent and ultimately highly damaging were the European pigs [72] that are especially destructive in wet and mesic forests, and goats and sheep that denude drier and more upland areas by their browsing [73–75]. The Hawaiian Islands are larger than many other Pacific oceanic archipelagos, such that it was possible for major sugar and pineapple plantations to be established over large areas, beginning during the nineteenth century; these industries persisted until the end of the twentieth century when they collapsed precipitously, faced by an inability to compete with much lower labour costs elsewhere [76,77]. Along with the cattle ranches, one of which is among the largest in the United States [78], endemic Hawaiian snails that were adapted to forest habitats could not survive in the monoculture plantations nor in the vast tracts of open pasture, although a remnant population of an endangered achatinelline tree snail, *Partulina physa*, was reported from an area of pasture in which tall native trees remained [79]. This destruction was probably an important cause of the demise of many of the more than 300 species of the Hawaiian endemic family Amastridae [19]. Rapid urban and suburban development and spread eventually further destroyed low and mid-elevation habitats that

by then were largely if not completely dominated by non-native vegetation, with native habitat confined to higher elevations, and with native snails largely also thus confined. The spread of non-native invasive grasses in Hawaii, and elsewhere in the tropics, has facilitated an increasing frequency of wildfires of fundamentally anthropogenic origin, fire not having played a major ecological role historically in that location [80], and may have been responsible for the extinction of land snails, although this has not been reported.

Deforestation and other forms of habitat loss or modification have had a profound impact across many other islands and archipelagos of the Pacific, beginning with deforestation by the original Pacific Islanders, and by even more extensive and catastrophic habitat loss following Western colonization. On Rapa (Austral Islands), an island of only approximately 40 km² but with about 100 endemic land snail species, only 13% of the forest cover remains ([81]; figure 3), with similar loss on many other Polynesian islands [63]. When the Mangarevan expedition of the Bishop Museum (Honolulu) visited the Gambier Islands in 1934, only a very small fragment of native forest remained on 26 km² of emerged land [82]. On Rarotonga (Cook Islands), the study of Brook [83] increased known past diversity from 23 to 37 species, but the proportion of documented extinctions increased from 22 to 49% [17]. Overall, this destruction has led to the extinction of many island endemic land snail species and, in some cases extinction of almost the entire land snail fauna of an island, for example, in French Polynesia [17,18,84–86], Henderson in the Pitcairn group [87] and the Galápagos [60]; indeed, most Pacific islands have been impacted by such loss to a greater or lesser extent. In New Caledonia, habitat loss has drastically fragmented populations of *Placostylus* species, although as yet none has gone extinct [88]. And the exquisite Manus Island (Papua New Guinea) green tree snail, *Papustyla pulcherrima*, is threatened mostly by deforestation, while collecting for international trade (below) appears to have declined [89]. In most cases of loss of the native snail faunas of Pacific islands, the fauna has been replaced by a suite of widespread species introduced via anthropogenic activities, many of them from beyond the Pacific Basin [90,91].

Widespread introduction of *Lissachatina fulica*, the giant African snail (figure 4), while a pest and general nuisance itself [92], has had the indirect impact of prompting the deliberate but ill-conceived introduction of predatory snails that prey on other snails in efforts to control it but that proved to play a key role in the demise of many native and endemic snail species [93,94]. Most notorious among these is *Euglandina 'rosea'* (figure 4), now known to be a species complex with perhaps as many as ten distinct lineages in their native southeastern United States [95]. Similarly, another snail predator, the flatworm *Platydemus manokwari* (figure 4), was deliberately introduced to several islands, both officially and unofficially, for the same purpose and with similar consequences in some cases [20]. In Taiwan, for example, *L. fulica* was deliberately introduced in 1932, followed by *Euglandina* in the 1960s, also introduced deliberately, and *P. manokwari*, either deliberately or inadvertently, by 2014 [14]. A comprehensive global review of all introductions of *Euglandina* and *P. manokwari* is available [14]; for more detail on the direct impacts of these invasive predators, and others, on native/endemic island land snail faunas, see §2b(ii).

While Pacific Islands have seen more mollusc extinctions than any other geographical region [20,32], further afield, the same essential trajectory towards extinction, resulting primarily from habitat destruction and often interwoven with the effects of invasive species, has played out. In Cuba, for example, precious hardwood extraction began in the sixteenth century and increased steadily into the first half of the twentieth century, when these woods were used primarily in carpentry and construction. However, beginning in the 1960s their use increased as their popularity among commercial craft workers and sculptors increased, leading to extensive habitat fragmentation by deforestation (only 14% remains) and risk of extinction of not only the native tree species but also the endemic snails that depend on them, most notably the spectacularly colourful and variable species of *Polymita* (figure 5) but also of *Liguus* [97]. In addition, because of their beauty, they are in great demand among shell collectors (see §2b(iii)).

Also in the Caribbean, Jamaica supports a highly diverse endemic snail and slug fauna, with over 560 species of which 90% are endemic [98]. However, similar to Cuba, less than 15% of the original forest remains, although 90% of the land snail species may still be extant, in much contracted ranges and with many persisting only in secondary forest; colourful urocoptid tree snails (*Anoma* spp.) are the most critically endangered, with some probably extinct [98].

In the Atlantic, Porto Santo and Madeira, in the Madeiran archipelago, previously uninhabited, were colonized by Europeans in 1419 and 1420, respectively, leading to deforestation and agriculture as well as the introduction of rabbits, cows, goats and pigs, as well as partridges and pigeons, as summarized by Goodfriend *et al.* [99]. It is possible that habitat modification began a century earlier, as there are records of visiting ships, and it is possible that these visitors left animals and plants on the islands to be available on future visits [99], as was done by early European visitors to the Hawaiian Islands [71]. It is also possible that mice were introduced to Madeira earlier still, perhaps by the Vikings [100]. More than 30% of the known fossil fauna of the two islands is extinct [22]. The essentially uninhabited Desertas Islands (figure 6) constitute the third component of the Madeiran archipelago. However, since the end of the fifteenth century significant habitat degradation is thought to have taken place on the Desertas as a result of occasional human activity, including goat and rabbit introductions, conifer plantation and agriculture; rabbits have now been eradicated, but goats, as well as mice, remain; the terrain is barren, sparsely vegetated with much bare rock and little soil [22]. Of the snail species known as fossils, 18 of 45 are now extinct [22].

The South Atlantic island of St. Helena has suffered almost complete destruction of the native vegetation, initially by introduced goats once the island had been discovered by the Portuguese in 1502, leading in places to severe erosion; the remaining trees were cut down by English settlers beginning in 1659 and some areas were cleared and pasture created using grass seeds from England; and finally, in the nineteenth and twentieth centuries, deliberate introduction of non-native plants increased, many of them becoming invasive, along with their associated insect and other pests [101]. In 1892, Smith [102] concluded that 27 'indigenous' (presumably endemic) land snail species were known from St. Helena but only seven were extant at that time as a result of the deforestation. The endemic *Succinea sanctahelenae* was assessed as Near Threatened by the IUCN in 1996 [103] and should be re-assessed, while another endemic, *Helenoconcha relicta*, was assessed as Critically



Figure 2. Mid-elevation ancient Hawaiian terraced field system (photo: N.K. Lincoln, with permission).



Figure 3. Left, almost total deforestation on the island of Rapa (Austral Islands) (photo: B. Fontaine). Right, deforestation for agriculture on Anjouan (Comoro Islands) (photo: B. Fontaine).

Endangered by the IUCN in 2014 [104]; it was not included by Smith [102] as it was not described until 1977. These two species appear to be the only remaining endemic snail species on St. Helena.

In São Tomé and Príncipe, deforestation has been considered a major threat to the endemic Obô giant snail, *Archachatina bicarinata* [105]. In Madagascar, despite the extensive loss of native forest and the strong probability that many of the over 1100 native snail species have gone extinct as a result and many more are threatened, surprisingly, none has been confirmed as extinct [106]. It is possible that without further intensive malacological surveys, many of the presumed already extinct species and those that go extinct in the future will never be discovered, or even described and named, especially as many Malagasy land snails are very small and their shells may readily disintegrate. However, just north of Madagascar, the land snail fauna of Mayotte in the Comoro Islands has suffered no extinctions [107]. Yet although no extinction has been documented in the other Comoro islands, these islands have suffered one of the highest deforestation rates in the world [108] (figure 3), and have a rich, though poorly documented, endemic land snail fauna with at least 130 species [109,110]. A high proportion of species listed by Fischer-Piette & Vukadinovic [110] in 1974 were not found during three field missions in the 2010s [109], suggesting that it is highly likely that extinctions have occurred there but remain undocumented.

By contrast, the Mascarene Islands (Mauritius, Rodrigues and Réunion), due east of Madagascar, have suffered extensive habitat transformation, although Réunion considerably less so than Mauritius and Rodrigues [1,111–113]. The Portuguese were



Figure 4. Top—*Lissachatina fulica* mating, Hawaii. Shell lengths *ca* 7–8 cm (photo: R.H. Cowie). Middle—*Euglandina* sp., Hawaii. Shell length *ca* 3 cm (photo: K. Kakuda, with permission). Bottom—*Platydemus manokwari*, head on right, Ogasawara Islands. Length: *ca* 8 cm (photo: S. Sugiura, public domain).



Figure 5. Left—diverse shell colours and patterns of *Polymita picta*; voted International Mollusc of the Year by the global malacological community, leading to the sequencing of its draft genome [96]. Right—*P. picta* shells used to make necklaces (photos: B. Reyes-Tur, with permission).

the first Europeans to visit the islands, in the sixteenth century, but forest destruction only began in the seventeenth century when the islands were colonized by the Dutch and only became widespread in the early eighteenth century after French colonization, peaking in the 19th century and continuing into the twentieth century [1,114,115]. The islands supported *ca* 170 native land snail species, of which 80–90% are endemic to the archipelago [1]. Extinction of this fauna began soon after the islands were settled by people and deforestation began [1,113], although some subfossil shells of extinct species have been dated much earlier than this at 2500–1000 yr BP [116]. Mauritius, the oldest and most disturbed island, supported 125 native species of which 81 were endemic to the island; 43 are now extinct, including 36 endemics [1,113]. Rodrigues had 30 native species, including 16 endemic to the island; 7, including 5 endemics, are extinct [1,113]. However, Réunion, as a consequence of having been far less deforested, has lost a much smaller proportion of the fauna: there were 58 native species, including 20 Réunion



Figure 6. In the foreground, the south plateau of Bugio, the southernmost island of the Desertas sub-archipelago, with Deserta Grande in the distance (photo: T. de Zoeten, with permission).

endemics, but only 4 are extinct [1]. In addition, predation by introduced predators has been implicated in the extinctions (§2b(ii)).

In the Seychelles, north of the Mascarenes, records of ecological change are limited. Until relatively recently, the forest ecosystems of the biggest island, Mahé, were fairly intact, until in the 1960s mid-elevation forests were cleared for tea and timber plantations [117]. Nonetheless, although secondary, much of the forest cover remains [117]. Of the 69 recorded native land snail species in the islands (including 52 endemic), only three have been considered extinct, and two of these were limited to lowland and only found as subfossils [118]. Forest clearance and forest fires shortly following colonization in the late eighteenth to early nineteenth centuries were considered the cause of the extinction of *Pachnodus ladiguensis* and *P. curiosus*, respectively [118]. The third species, *P. velutinus*, went extinct in 1994 as a result of hybridization with *P. niger* to the extent that no pure *P. velutinus* could be found, the expansion of the range of *P. niger* possibly being brought about by environmental change [117,118].

(ii) Direct impacts of invasive species

While invasive plants can be the architects of habitat change by replacing native vegetation, and while invasive herbivorous animals may facilitate this through grazing and browsing, other invasive animals may also be important as predators and/or competitors of native species.

The Polynesian rat, *Rattus exulans*, was spread widely through the Pacific by early Polynesian people, but to what extent these rats preyed on native snails, if at all, is unclear [16,68,119], although in New Zealand predation of *Placostylus ambagiosus* by *R. exulans* is apparent in the fossil record [120]. Much later, introductions of *Rattus rattus* and *R. norvegicus* [121], especially the former, which is a significant predator of snails, led to further loss, notably of the endemic and spectacularly colourful achatinelline tree snails in the Hawaiian Islands [16,70]. In New Caledonia, rats, along with feral pigs, are considered to have had the most severe impact on species of *Placostylus* [88]. In the Ogasawara Islands, *R. rattus* predation altered land snail species assemblages significantly [122]. Predation by both *R. rattus* and/or *R. norvegicus* has been suggested as possibly implicated in part as a cause of post-1860s land snail decline on Rarotonga (Cook Islands) [83]. These are but a few examples of snail predation by rats, which is probably ubiquitous.

Perhaps worse than the accidental introduction of rats, however, has been the deliberate introduction of predatory snails that prey on other snails, as noted above. Most notorious has been *Euglandina* (figure 4), initially introduced to the Hawaiian Islands in 1955 [123]. Two species of the *Euglandina* complex, neither of which has yet to be confirmed as true *E. rosea*, are present in the Hawaiian Islands and have been distributed to several islands and archipelagos across the Pacific and elsewhere [14,95]. The purpose of their introduction, along with a suite of other carnivorous snail species that prey on other snails, including *Gonaxis kibweziensis* and *G. quadrilateralis* brought in from East Africa [124], was as biocontrol agents intended to control burgeoning populations of the giant African snail (*L. fulica*) (figure 4), although most of the introduced species did not become established. *Lissachatina fulica* had been introduced to the Hawaiian Islands initially in 1936 [123] and had become a significant horticultural and garden pest and general public nuisance, although perhaps less of an agricultural pest than often mentioned [92,94].

Soon thereafter, *L. fulica* was introduced, mostly inadvertently, to many islands across the Pacific [14,90], often becoming such a nuisance that authorities resorted to the introduction of *Euglandina* as a putative biocontrol agent, in some cases on

the recommendation of agriculture authorities in Hawaii. However, despite what some authors concluded [124,125], there is no clear evidence that *Euglandina* could impact *L. fulica* at a population level; yes, it would prey on small *L. fulica*, but the reproductive capacity of *L. fulica* is such that the predation by *Euglandina* had no long-term impact on its populations [90,93]. But the slow-growing, slow-reproducing and ovoviviparous partulid and achatinelline tree snails, which probably evolved in the absence of significant predation, were another matter [15]; a short-lived bout of predation by *Euglandina* might kill just a few tree snails, but it would take years for the population to replace them [70,126]. A key observation was made in the Society Islands of French Polynesia, when *L. fulica* populations on Huahine declined at the same time as those on Moorea and Tahiti, even though *Euglandina* had not been introduced to Huahine [127]. Eventually, all species of *Partula* in the Society Islands, except those on Tahiti, were considered extinct in the wild [128], although *P. meyeri* was subsequently found alive and formally described [129] and a molecular genealogical study has demonstrated survival of multiple lineages within several of the traditional species that survived in captivity [130]. Although the devastating impact of *Euglandina* on large endemic land snail species such as partulids and achatinellids is well documented, its impact on small to minute endemic species is completely unknown but might be as important, since *Euglandina* may even prefer such species, including endemic ones [131–133]. In contrast, in New Caledonia, *Euglandina* has not become widely established and has not had such devastating impacts [88]. And in Mauritius, *L. fulica* was not a preferred prey of *Euglandina* based on stomach content analyses [131].

In the Atlantic, *Euglandina*, as well as *G. quadrilateralis* and *G. kibweziensis*, have only been introduced to Bermuda, from Hawaii between 1958 and 1972 [43]. These introductions were intended for control of two other introduced snail species, *Rumina decollata*, accidentally introduced in the 1870s with imported plants and a facultative snail predator itself [93], and *Otala lactea*, introduced initially for food in 1928 but escaped; both became agricultural pests [43]. The intended control by *Euglandina* in particular was not successful, but the drastic decline of species in the endemic genus *Poecilozonites* was attributed to it [42,43].

In the Indian Ocean, *Euglandina* has been introduced to Madagascar, the Comoros and Mascarene Islands, the Seychelles and the Andaman and Nicobar Islands. But in no case was *Euglandina* explicitly implicated in land snail extinction, with the exception of a statement that any impact on native snails could not be clearly disentangled from declines caused by other predators, including rats, tenrecs and toads, and by habitat degradation [14], and a general mention that *Euglandina* has been responsible for many extinctions on oceanic islands, implying that it could be a threat on Réunion [134]. This lower impact of *Euglandina* could be because several carnivorous streptaxid land snail species are native to these islands, such that the indigenous species may have been better adapted to resist *Euglandina* predation [14].

More recently, the flatworm *Platydemus manokwari* (figure 4), native to New Guinea and another voracious snail predator [135], has been widely introduced [14], in most cases probably inadvertently, perhaps associated with horticultural products [136], but also in deliberate biocontrol efforts against *L. fulica* [137]. On Chichijima, the largest of the Ogasawara Islands of Japan, roughly 1000 km south of Tokyo, *P. manokwari* invaded in the 1990s [138] (not the 1960s as reported by Gerlach *et al.* [14]), expanding its range through the 2000s and rapidly exterminating almost the entire land snail fauna of the island. On Guam, *P. manokwari* may have been present by 1969, but by 1977 it was well established and by 1980 had spread to the entire island and has been implicated in the declines of not only *L. fulica* but also *Euglandina* and *Gonaxis* populations [14,139]. Similarly, in the Northern Mariana Islands, north of Guam, although the populations of *L. fulica* declined, the implication that this was a result of predation by predatory snails and *P. manokwari* was questionable [14]. Predation by *P. manokwari* on Rotuma (Fiji) was suggested as an explanation for the high proportion of native snail species found only as empty shells [140]. In the Maldives, intentionally introduced *P. manokwari* were said to have controlled populations of *L. fulica*, even though declines of those populations also occurred on islands on which the flatworm was not established [141]. And in the Society Islands, *P. manokwari* has significantly hindered the release and survival of captive-reared *Partula* tree snails (see §3).

For a more comprehensive global review of the introductions and impacts of both *Euglandina* and *P. manokwari* on native/endemic snails, see Gerlach *et al.* [14].

Other flatworms have been reported as introduced in several islands in the Pacific [14]. In the Ogasawaras, on islands other than Chichijima, unidentified species of *Platydemus*, *Bipalium* and *Australopacifica* have been suggested as causing the declines of native snails. And in Bermuda, *Bipalium vagum* and *Gigantea gubernoni*, as well as a nemertine (ribbon worm), *Geonemertes pelaensis*, have been strongly implicated in extinction of endemic land snails [142]. *Endeavouria septemlineata* (as ‘*Geoplana*’) feeds on snails and in Hawaii it may pose a threat to native species [70] but this has not been ascertained definitively.

Invasive ants have also been implicated, most notably by Solem [143,144], in the decline, extirpation and extinction of island land snails (although he mentioned no particular ant species), and specifically with regard to Pacific island Endodontidae. Three ant species (*Anoplolepis gracilipes*, *Paratrechina longicornis*, *Pheidole megacephala*) have been suggested as possibly having contributed to land snail extinction in the Cook Islands [91].

Jackson’s chameleons (*Trioceros jacksonii*), introduced to the Hawaiian Islands in the early 1970s associated with the pet trade, rapidly spread throughout most of the islands [145]. The chameleons readily prey on snails and may have population-level impacts on endemic snails [145,146].

By contrast to the clear impacts of predation on native snail species by invasive species, there is no clear evidence for competition with invasive species as a cause of extinction of island land snails. Nonetheless, this cannot be excluded, since the land snail fauna of many tropical islands is now dominated by a small set of non-native species, often in the subfamily Subulininae (Achatinidae), which are almost ubiquitous in the tropics. Whether their success is a cause or a consequence of the almost complete extinction of native land snails is unclear, but competition between native and introduced land snails remains a possibility. For instance, competition from the non-native snail *Cornu aspersum* has been suggested tentatively as a contributing factor (along with exploitation and climate change—see §§2b(iii,iv)) in the extirpation of the native snail *Helix godetiana* from 22 of the 32 Aegean islands on which it was historically present [147]. In São Tomé and Príncipe, competition

between endemic *Archachatina bicarinata* and invasive *A. marginata* has been hinted at [105]. And in the Pacific, it has been speculated that introduced subulinines may compete with native litter-dwelling snails [148].

(iii) Exploitation and collecting

Snails are well known and popular food resources in many parts of the world, although few island species are widely eaten. In the Aegean islands, *H. godetiana* is eaten by people, as are several other species around the Mediterranean, and this, along with competition (above) and anthropogenic climate change (below), may have contributed to its disappearance from many of the islands on which it once occurred [147]. In New Caledonia, vast numbers of *Placostylus fibratus guestieri* ('escargots de l'Île des Pins') were collected for human consumption, prompting regulations to restrict collecting; although not facing extinction, there is concern for the sustainability of the resource [88]. However, harvesting *A. bicarinata* for food on the islands of São Tomé and Príncipe has been considered a major threat, along with an unknown disease from which the snails suffered [149] as well as deforestation and perhaps competition with invasive *Archachatina marginata* (above).

Of more concern, especially in the Pacific, has been the use of snail shells for ornamental purposes and, importantly, the activities of shell collectors, who value the most colourful, large and rare species; for these species, collecting may have had a significant impact on the populations. Shells are used widely for necklaces, hat decoration and other ornamentation (figure 7) (e.g. [64,150]). The first Hawaiian land snail species to be described and named by Western science, in the report by Dixon [151] of his voyage around the world, was based on shells of *Achatinella apexfulva* in a necklace obtained in Hawaii from native Hawaiian people. This species was also the most recent to go extinct, when the last known individual died in captivity [152]. Thousands of shells of the partulid tree snail *Eua zebrina* adorned the chandeliers in the former Rainmaker Hotel in American Samoa (figure 7), and their collection surely had a significant impact on the populations [64,153]. In Hawaii, collecting notes and recorded comments from the 1850s to the early 1900s document the collection of thousands upon thousands of achatinelline tree snails (mostly *Achatinella* and *Partulina*) in just a few hours on multiple occasions, which surely had population-level effects [70]. The IUCN Red List includes 79 achatinellines, but only *Achatinella* species are listed in CITES Appendix I [154], which is for species threatened with extinction and for which trade is permitted only in exceptional circumstances.

In eastern Cuba, the equally if not more colourful species of *Polymita* (figure 5) have been collected and traded extensively, though illegally [155], while also facing habitat fragmentation resulting from both deforestation (above) and climate change (below). None of these *Polymita* species has been evaluated by the IUCN, but all are listed in CITES Appendix I [154], and previously Appendix II, based on the extent of the trade [156]. The Manus Island (Papua New Guinea) green tree snail, *Papustyla pulcherrima*, is listed as Near Threatened on the Red List, primarily because of habitat destruction from deforestation (above), but although harvest for illicit international trade is occurring, it is thought to have declined and the species is listed in CITES Appendix II. These three taxa, *Achatinella* spp., *Polymita* spp. and *P. pulcherrima*, are the only land snails listed in the CITES appendices.

(iv) Human-caused climate change

The only species of land snail to have been considered extinct as a result of anthropogenic climate change is *Rhachistia aldabrae*, endemic to Aldabra [157], but it was subsequently rediscovered alive [158]. It remains listed by the IUCN [29] as Critically Endangered.

Ecological niche modelling of the potential ranges under climate change of five of the six species of Cuban *Polymita*, which exhibit perhaps the most beautiful shell colour and pattern polymorphism of any land snails, suggested that four of them should be considered Endangered and one Vulnerable [159].

In the Aegean Islands, the absence of *Helix godetiana* from islands where it was previously present, even abundant, has been suggested, among other causes (above), as having resulted in part from its reproductive strategy having been well-adapted to the climatic conditions of several millennia ago, when the area was less arid and had higher levels of precipitation in the spring [147]. Unlike most other Aegean island snails, which tend to lay their eggs after the onset of the autumn rainy season, *H. godetiana* lays its eggs at the end of spring, with hatchlings then forced to survive the hot, dry summer. As the modern climate warms increasingly, the remaining populations of *H. godetiana* may be seriously threatened.

Several studies have addressed the possibility of extinction, as the climate warms, of land snails that are confined to cooler climates at higher elevations as the available suitable habitat declines and vanishes. In a study of a suite of species occurring from 100 to 900 m elevation in Pennsylvania, USA, five occurred significantly more often at higher, cooler elevations, and these might become threatened as the climate warms [160]. In Australia, two species belonging to a high-elevation dry rainforest land snail community recognized as being of outstanding conservation significance are listed as Endangered (*Triboniophorus* sp. nov. 'Kaputar') and Data Deficient (*Cralopa kaputarensis*) by the IUCN, with anthropogenic climate warming of this isolated mountain top community being the most significant threat [161,162]. In the Society Islands (French Polynesia), global warming could raise the upper altitudinal limit of introduced *Euglandina*, thus putting at risk endemic species restricted to the higher summits, such as *Nesoropupa* spp. [163].

Climate change, resulting in more frequent and more powerful tropical cyclones, may also increase the threat to island biodiversity in general, according to a study of vertebrates in five insular biodiversity hotspots [164] and by an assessment of the potential effects on biodiversity in general in the Caribbean [12]. It seems reasonable to conclude that land snails of these hotspots (Japan, Polynesia–Micronesia, Philippines, Madagascar and the Indian Ocean Islands, Caribbean Islands) might face the same threat. However, a study of land snails of an island in Palau (western Pacific) before and after a typhoon [165] found that ten of twelve species known on the island survived the typhoon; the other two may have survived but were not found,



Figure 7. Top: Necklace bought in 2003 in the airport on Rurutu (Austral Islands, French Polynesia), where these were openly sold to tourists despite legal protection; the white shells are *Partula hyalina* (Photo B. Fontaine). Bottom: One of the chandeliers in the former Rainmaker Hotel, American Samoa. The chandeliers contained an estimated 10 000 *Eua zebrina* (Partulidae) shells (photo R.H. Cowie).

either because of local extinction, difference in collecting effort before and after and/or sampling sites that differed before and after the event. The authors concluded that severe storms may not be a serious threat, although this may be an unwarranted generalization as it remains possible that the two species that were not found could indeed have been extirpated entirely from the island.

3. Conservation

Major conservation programmes have been implemented for several important island land snail faunas, notably involving captive breeding and subsequent release into the wild when conditions for survival improve.

The first and most developed of these programmes is that to save the partulid tree snails of the Pacific islands, especially those of French Polynesia. With the release of *Euglandina* spp. as a putative biocontrol agent against the giant African snail *L. fulica* in the Society Islands in 1977 and the almost immediate precipitous decline of partulids, especially on Moorea and Tahiti, as discussed above (§2b(ii)), in 1986 a captive breeding programme was initiated to establish *ex situ* populations of as many partulid species as possible [166,167]. This programme now involves 15 zoos in 5 countries (Germany, Latvia, Poland, UK and USA), thereby limiting the risk of a calamitous event destroying every individual, and major efforts are ongoing to release captive-bred snails into forests on several of the Society Islands, where so far more than 30 000 individuals of 14 species have been released (figure 8). A handbook of best practice guidelines for maintaining *Partula* populations in captivity is available [168], and progress reports are published most years in the annual IUCN Mollusc Specialist Group newsletter, *Tentacle* [169–173]. The main hindrance seems to be the presence of *Platydemus manokwari* rather than *Euglandina* at the release sites, although it seems that *Partula* can be re-established even with some level of active predation [172]. But invasion by little fire ants, *Wasmannia auropunctata*, appears to have displaced the population of one of the *Partula* species [172]. An effort was made in 1994 to establish partulid populations in a predator-proof enclosure on Moorea, into which captive-reared snails were released, but

while promising initially, the logistics of monitoring and maintaining the enclosure proved too difficult to overcome and the effort was abandoned in 1998 [174]. Another enclosure was set up in Tahiti a few years later and was abandoned in 2015, for the same reasons [175]. The failure of the enclosure approach did not stop reintroduction attempts, and *Partula* have been released directly onto native trees in several of the Society Islands every year since 2016 (excluding 2020–2022), with over 32 000 snails being returned to the wild and some populations newly established [172].

Achatinellinae in the Hawaiian Islands are the ecological equivalents of Partulidae in the South Pacific, although they are even more slow-growing and slow-reproducing [15]. *Ex situ* populations were initially established on the island of Oahu between 1991 and 2000 [176], initially at the University of Hawaii in Honolulu, but the programme is now much expanded with over 40 species in captivity, not only achatinellids but also amastrids, endodontids and heliciniids. The ‘Snail Extinction Prevention Programme’ (SEPP) was established in 2012 [177] and is overseen by the State of Hawaii Department of Land and Natural Resources, with colonies now distributed over three facilities in Honolulu—the main SEPP facility, the Bishop Museum and the Honolulu Zoo—to reduce risk of loss in the event of a fire, hurricane, disease outbreak, etc. Following the unsuccessful attempt to establish partulid populations in an enclosure on Moorea, two similar enclosures were built on Oahu in 1998 (D.R. Sischo 2025, personal communication), to surround two isolated populations of the achatinelline tree snail *Achatinella mustelina* [176,178]; there are now 14 such enclosures, on the islands of Oahu (11), Maui (1) and Lanai (2), with ten new ones in various stages of planning and construction (D.R. Sischo 2025, personal communication). The enclosures are designed to exclude rats, Jackson’s chameleons and *Euglandina* (figure 9), which remain significant predators in the natural habitat. *Platydemus manokwari* is present in Hawaii but has not become widespread and abundant and would probably be excluded by the electric barrier. Small cages are used for protecting ground-dwelling species [177]. A trained dog is now being used to detect *Euglandina* incursions into the enclosures and to detect chameleon faeces that would indicate the presence of chameleons in the vegetation within the enclosures [179]. Regular reports are published in *Tentacle* [177,179–182].

In the Ogasawara Islands of Japan, a nascent captive rearing programme was initiated in 2002 for land snails in the genus *Mandarina* [183]. Subsequently, the Ogasawara Islands were recognized as a UNESCO World Heritage Site in 2011 for their unique biodiversity, in particular, the radiation of *Mandarina* [20], and with this recognition, a new, state-of-the-art facility was built on Chichijima, the main and largest island, to house the captive breeding programme for the snails primarily of this island (figure 10). Again, updates on progress have been published in *Tentacle* since 2020 [184–187].

In the western Atlantic, the introduction of *Euglandina* to Bermuda led to the extinction of all but two of the species in the endemic Bermudan genus *Poecilozonites* [42,43]. In 1988, *P. circumfirmatus* was found alive, and only recently dead shells of *P. bermudensis* could be found. Subsequently, *P. bermudensis* was considered extinct, having last been seen alive in the 1990s, and *P. circumfirmatus* was thought to be extinct in the wild, having last been seen in 2004 when individuals were brought into captivity [142]. However, in 2014, a small population of *P. bermudensis* was found in a small alleyway in the city of Hamilton, but because of impending development, some individuals of this species were also brought into captivity [142]. Thus began a captive rearing effort undertaken in the UK, initially at the Zoological Society of London and subsequently at Chester Zoo. The snails have been prolific, and as of 2023 more than 111 000 snails from Chester Zoo have been reintroduced to over 20 sites in Bermuda, most, if not all, being free of predators, with ongoing monitoring confirming successful establishment at many of them [142,170,188].

More recently in the UK, Chester Zoo, in collaboration with Bristol Zoo, as well as ZooParc de Beauval in France, has also been heavily involved in captive breeding of four endemic land snail species of the Desertas Islands in the Madeiran archipelago: *Discula lyelliana*, *Geomitra grabhami*, *Atlantica calathoides* and *G. coronula* [170,189]. Three of the species have been especially prolific, producing over 3000 to 9000 offspring, with the fourth (*A. calathoides*) reproducing at a much slower rate [190]. The first releases, of 430 *D. lyelliana* and 900 *G. coronula*, took place in late 2024 on the island of Bugio (figure 6) that had been cleared of goats and mice, the causes of habitat loss and predation, respectively [190].

Also in the Atlantic, a recent on-island effort has been made to establish a captive breeding project for *Archachatina bicarinata*, endemic to the islands of São Tomé and Príncipe and listed by the IUCN as Endangered [105,149].

Finally, on Mauritius in the Indian Ocean, captive breeding of the endemic *Pachystyla bicolor* is being undertaken, with successful release and reproduction in predator-proof enclosures [191].

4. Conclusion

The trajectory of extinction on most of the islands discussed here has generally been very similar, once set in motion. In the Pacific, initial habitat destruction took place as the islands were discovered by the original Pacific island voyagers, over several thousand years as they spread from west to east across the ocean. Subsequently, with the arrival of Europeans, devastating forest clearing, habitat modification as a result of the introduction of more damaging invasive species, especially cattle, goats, sheep, European pigs and both black and brown rats, and eventually urban development on the larger islands led to the almost total transformation of many islands and the loss of many native/endemic species, including snails.

In the much smaller Caribbean, the history is nonetheless somewhat more complex. The first colonizers arrived from Central and South America, occupying the Greater Antilles around 6000 years ago. A subsequent wave around 2500 years ago from northern South America colonized the Lesser Antilles and, moving northwards, became the dominant group throughout the Caribbean [192]. The levels of destruction in the Caribbean by these original peoples are much less clear than they are in the Pacific, as the zooarchaeological record is less well known. After the arrival of Europeans the record of habitat destruction or modification is extensive, although despite this, few land snails have been reported as having gone extinct either as a result of human or non-human causes.

In the Atlantic and Indian Oceans, Europeans were the first to colonize the islands of Macaronesia and the Mascarenes, respectively. There were no prior native people, contrasting with the Pacific and the Caribbean. However, once Europeans had



Figure 8. Captive-reared and marked *Partula varia* shortly after release on Huahine (Society Islands) (photo: P. Pearce-Kelley, with permission).



Figure 9. Enclosure in Hawaiian forest, designed to protect endemic Hawaiian snails from predation by rats, chameleons and *Euglandina*. Inset: the last known individual of *Achatinella apexfulva*, the first *Achatinella* species to be described scientifically—known as ‘George’ after the last Pinta Island Galapagos tortoise—died in captivity on 1 January 2019, aged 14 (photos: D.R. Sischo, with permission).

arrived, the same train of destruction took place, with extensive deforestation, introduction of non-native species and decline and extinction of native species, including land snails.

Globally, as has often been noted, island land snails constitute a major proportion of known extinct species, with the islands of the Pacific contributing the most significant component [32]. It may be the case that this pattern reflects the vast land snail diversity of islands, many of the species being single island or single archipelago endemics, especially in the Pacific, as well as the greater extent of dedicated survey work undertaken on Pacific islands, extending back to the mid-nineteenth century, through the early twentieth century to the present day.

Despite the devastation, there remains some scope for preservation of what is left of these unique island snail faunas. Specifically targeted captive rearing programmes continue to preserve a small proportion of the species, primarily in the Pacific, where habitat destruction has been the most severe and extensive; *in situ* conservation of endemic island snails appears to be possible in only rare cases, but habitat conservation efforts, especially in the Indian Ocean, where extensive native forest is still



Figure 10. The new land snail captive rearing, exhibition and educational facility in Chichijima, Ogasawara Islands. Left—main entrance. Right—rearing room. (Photos: Ogasawara Ranger Office, with permission.).

present on some islands (e.g. Réunion, Mahé), could still permit the survival of some species in their natural habitats. Habitat restoration, however, will not help to stem the extinction of land snails unless the alien predators that prey on them are removed on a landscape scale, which is not on the foreseeable horizon, or unless they decline naturally to a level sufficiently low to permit adequate survival of reintroduced captive-reared snails. There are, however, notable initiatives for *in situ* conservation that can buy time—e.g. predator-proof enclosures [179] and protecting release trees with barriers of cloth soaked in salt solution [172]—and offer a glimmer of hope for a positive outcome.

Island biotas are key for discovering and protecting a major component of global biodiversity [5,193] and their loss should not be discounted as ‘regrettable’ [194] or otherwise downplayed [195,196]. Concerted and targeted field work to find and collect representative specimens of remaining species is needed in order that knowledge of the existence of these diverse faunas be available for posterity [33]. The prospects are not good and much of the damage has already been done. Nevertheless, documenting what remains, including as yet undiscovered species, and preserving what can be saved constitute the priorities for island snail conservation globally.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. R.H.C.: conceptualization, investigation, visualization, writing—original draft, writing—review and editing; P.B.: conceptualization, investigation, writing—original draft; B.F.: conceptualization, investigation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. No funding has been received for this article.

Acknowledgements. We thank the guest editor, Mark Williams, for the invitation to contribute to this special issue. We thank Paul Pearce-Kelley for information about the *Partula* Conservation Breeding Programme and David Sischo for information about the Hawaiian Snail Extinction Prevention Program. We also thank Owen Griffiths, Justin Gerlach and Vincent Florens for help with literature on the Seychelles and Mascarene islands, and we thank all those who contributed or facilitated access to photographs, as credited in the figure legends, as well as Mayu Inada, Julia Sigwart and Dinarte Teixeira. For comments on all or part of a draft, we thank Tim Pearce, Noa Lincoln and an anonymous reviewer. Publication number 12058 of the University of Hawaii School of Ocean and Earth Science and Technology.

References

- Griffiths OL, Florens VFB. 2006 *A field guide to the non-marine molluscs of the Mascarene Islands (Mauritius, Rodrigues and Réunion) and the Northern dependencies of Mauritius*. Mauritius: Bioculture Press.
- Higgins MD. 2009 Greek islands, geology. In *Encyclopedia of Islands* (eds RG Gillespie, DA Clague), pp. 392–396. Berkeley, CA, Los Angeles, CA, London, UK: University of California Press. (doi:10.1525/9780520943728-092)
- Stelbrink B, Albrecht C, Hall R, von Rintelen T. 2012 The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace’s ‘anomalous island’? *Evolution* **66**, 2252–2271. (doi:10.1111/j.1558-5646.2012.01588.x)
- Culek M. 2013 Geological and morphological evolution of the Socotra Archipelago (Yemen) from the biogeographical view. *J. Landsc. Ecol.* **6**, 84–108. (doi:10.2478/jlecol-2014-0005)
- Fernández-Palacios JM *et al.* 2021 Scientists’ warning – the outstanding biodiversity of islands is in peril. *Glob. Ecol. Conserv.* **31**, e01847. (doi:10.1016/j.gecco.2021.e01847)
- Xiang HQ, Lu YZ, He YM, Li CY, Gao H, Lv AS, Chen H. 2025 Twenty-seven new species and four new genera of Gastropoda (Animalia: Mollusca) from plateau lake quaternary sediments in Yunnan, southwestern China. *Ecol. Montenegrina* **84**, 48–71. (doi:10.37828/em.2025.84.6)
- Clements R, Sodhi NS, Schilthuizen M, Ng PKL. 2006 Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *Bioscience* **56**, 733–742. (doi:10.1641/0006-3568(2006)56[733:lkosaj]2.0.co;2)

8. Meyer WM *et al.* 2015 Ground-dwelling arthropod communities of a Sky island mountain range in Southeastern Arizona, USA: obtaining a baseline for assessing the effects of climate change. *PLoS One* **10**, e0135210. (doi:10.1371/journal.pone.0135210)
9. Wood JR *et al.* 2017 Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environ. Conserv.* **44**, 348–358. (doi:10.1017/s037689291700039x)
10. Cowie RH, Holland BS. 2006 Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J. Biogeogr.* **33**, 193–198. (doi:10.1111/j.1365-2699.2005.01383.x)
11. Trewick SA, Cowie RH. 2008 Evolution on Pacific islands: Darwin's legacy. *Phil. Trans. R. Soc. B* **363**, 3289–3291. (doi:10.1098/rstb.2008.0127)
12. Gould WA, Castro-Prieto J, Álvarez-Berrios NL. 2020 Climate change and biodiversity conservation in the Caribbean Islands. In *Encyclopedia of the world's biomes* (eds MI Goldstein, DA Dellasala), pp. 114–125, vol. 1. Elsevier. (doi:10.1016/B978-0-12-409548-9.12091-3)
13. Goodman SM. 2023 Updated estimates of biotic diversity and endemism for Madagascar—revisited after 20 years. *Oryx* **57**, 561–565. (doi:10.1017/s0030605322001284)
14. Gerlach J *et al.* 2021 Negative impacts of the invasive predators *Euglandina 'rosea'* (Mollusca: Spiraxidae) and *Platydemus manokwari* (Platyhelminthes: Geoplanidae) when used as biological control agents against the pest snail *Lissachatina fulica* (Mollusca: Achatinidae). *Biol. Invasions* **23**, 997–1031. (doi:10.1007/s10530-020-02436-w)
15. Cowie RH. 1992 Evolution and extinction of Partulidae, endemic Pacific island land snails. *Phil. Trans. R. Soc. Lond. B* **335**, 167–191. (doi:10.1098/rstb.1992.0017)
16. Hadfield MG, Miller SE, Carwile AH. 1993 The decimation of endemic Hawaiian tree snails by alien predators. *Am. Zool.* **33**, 610–622. (doi:10.1093/icb/33.6.610)
17. Richling I, Bouchet P. 2013 Extinct even before scientific recognition: a remarkable radiation of helicinid snails (Helicinidae) on the Gambier Islands, French Polynesia. *Biodivers. Conserv.* **22**, 2433–2468. (doi:10.1007/s10531-013-0496-2)
18. Sartori AF, Gargominy O, Fontaine B. 2014 Radiation and decline of endodontid land snails in Makatea, French Polynesia. *Zootaxa* **3772**, 1–68. (doi:10.11646/zootaxa.3772.1.1)
19. Régner C, Bouchet P, Hayes KA, Yeung NW, Christensen CC, Chung DJD, Fontaine B, Cowie RH. 2015 Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction. *Conserv. Biol.* **29**, 1715–1723. (doi:10.1111/cobi.12565)
20. Chiba S, Cowie RH. 2016 Evolution and extinction of land snails on oceanic islands. *Annu. Rev. Ecol. Evol. Syst.* **47**, 123–141. (doi:10.1146/annurev-ecolsys-112414-054331)
21. Gerlach J. 2016 *Icons of evolution: Pacific island tree-snails, family Partulidae*. Cambridge, UK: Phelsuma Press.
22. Teixeira D, Groh K, Yanes Y, Pokryszko BM, Silva I, Cameron RAD. 2022 Late Quaternary land snail faunas of the Desertas Islands (Madeira): high diversity and endemism followed by recent impoverishment and extinction. *J. Molluscan Stud.* **88**, eyac010. (doi:10.1093/mollus/eyac010)
23. Pimm SL, Moulton MP, Justice LJ. 1994 Bird extinctions in the central Pacific. *Phil. Trans. R. Soc. Lond. B* **344**, 27–33. (doi:10.1098/rstb.1994.0047)
24. Solem A. 1984 A world model of land snail diversity and abundance. In *World-wide snails: biogeographical studies on non-marine Mollusca* (eds A Solem, AC van Bruggen), pp. 6–22. Leiden, The Netherlands: Brill/Backhuys. (doi:10.1163/9789004631960_004)
25. Cowie RH. 1996 Pacific island land snails: relationships, origins, and determinants of diversity. In *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes* (eds A Keast, SE Miller), pp. 347–372. Amsterdam, The Netherlands: SPB Academic Publishing.
26. Seddon MB. 2008 The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago. Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales. *Biot. Rep.* **2**, 1–196.
27. Rundell RJ. 2010 Diversity and conservation of the land snail fauna of the Western Pacific Islands of Belau (Republic of Palau, Oceania). *Am. Malacol. Bull.* **28**, 81–90. (doi:10.4003/006.028.0223)
28. Proios K *et al.* 2024 Functional diversity and community convergence of land snails in the Aegean Sea islands. *J. Biogeogr.* **51**, 1632–1645. (doi:10.1111/jbi.14740)
29. IUCN. 2025 The IUCN Red List of Threatened Species, Version 2025-1. See <https://www.iucnredlist.org>.
30. MolluscaBase eds. 2025 MolluscaBase. See <https://www.molluscabase.org> (accessed 8 August 2025).
31. Lydeard C *et al.* 2004 The global decline of nonmarine mollusks. *Bioscience* **54**, 321–330. (doi:10.1641/0006-3568(2004)054[0321:tgdonm]2.0.co;2)
32. Régner C, Fontaine B, Bouchet P. 2009 Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conserv. Biol.* **23**, 1214–1221. (doi:10.1111/j.1523-1739.2009.01245.x)
33. Cowie RH, Bouchet P, Fontaine B. 2022 The sixth mass extinction: fact, fiction or speculation? *Biol. Rev.* **97**, 640–663. (doi:10.1111/brv.12816)
34. Cowie RH, Régner C, Fontaine B, Bouchet P. 2017 Measuring the sixth extinction: what do mollusks tell us? *The Nautilus* **131**, 3–41.
35. Sohn JC, Labandeira C, Davis D, Mitter C. 2012 An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa* **3286**, 1–132. (doi:10.11646/zootaxa.3286.1.1)
36. Backus DH. 2025 Contemporary issues and advancements in coastal eolianite research. *J. Mar. Sci. Eng.* **13**, 321. (doi:10.3390/jmse13020321)
37. Stearns HT. 1970 Ages of dunes on Oahu, Hawaii. *Occasional Papers of Bernice P. Bishop Museum* **47**, 49–72.
38. Fletcher CH, Murray-Wallace CV, Glenn CR, Sherman CE, Popp B, Hessler A. 2005 Age and origin of late Quaternary eolianite, Kaiehu point (Moomomi), Molokai, Hawaii. *J. Coast. Res.* **42**, 97–112.
39. Vacher HL, Harty PJ, Rowe MP. 1995 Stratigraphy of Bermuda: nomenclature, concepts, and status of multiple systems of classification. *Geol. Soc. America Spec. Pap.* **300**, 271–294. (doi:10.1130/0-8137-2300-0.271)
40. Rowe MP, Bristow CS. 2015 Landward-advancing Quaternary eolianites of Bermuda. *Aeolian Res.* **19**, 235–249. (doi:10.1016/j.aeolia.2015.06.007)
41. Peile AJ. 1926 The Mollusca of Bermuda. *Proc. Malacol. Soc. Lond.* **17**, 71–98.
42. Gould SJ. 1991 Unenchanted evening. *Nat. Hist.* **9**, 4–14.
43. Bieler R, Slapcinsky J. 2000 A case study for the development of an island fauna: recent terrestrial mollusks of Bermuda. *Nemouria* **44**, 1–100.
44. Gould SJ. 1969 An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. Comp. Zool.* **138**, 407–532.
45. Cowie RH, Evenhuis NL, Christensen CC. 1995 *Catalog of the native land and freshwater molluscs of the Hawaiian Islands*. Leiden, The Netherlands: Backhuys Publishers.
46. Cooke CM Jr, Kondo Y. 1952 New fossil forms of *Carelia* and *Partulina* (Pulmonata) from Hawaiian Islands. *Occasional Papers of Bernice P. Bishop Museum* **20**, 329–346.
47. Mollusc Specialist Group. 1996a *Carelia bicolor*. The IUCN Red List of Threatened Species 1996: e.T3876A10148280. (doi:10.2305/IUCN.UK.1996.RLTS.T3876A10148280.en)
48. Cooke CM Jr. 1931 The land snail genus *Carelia*. *Occasional Papers of the Bernice P. Bishop Museum* **85**, 1–97, pls. i–xviii.
49. Severns M. 2009 A new species of *Newcombia* from the Pleistocene of Kaua'i, Hawaiian Islands, USA (Gastropoda, Pulmonata, Achatinellidae). *Basteria* **73**, 57–60.
50. Cooke CM Jr. 1917 Some new species of *Amastrea*. *Bernice Pauahi Bish. Mus. Polyn. Ethnol. Nat. Hist.* **3**, 221–250, pls. vi–vii.
51. Stearns HT. 1973 Geologic setting of the fossil goose bones found on Molokai island, Hawaii. *Occasional Pap. of Bernice P. Bishop Mus.* **24**, 155–164.
52. Neal MC. 1934 Hawaiian Helicinidae. *Bernice P. Bishop Mus. Bull.* **125**, 1–102.
53. Cooke CM Jr. 1933 New species of amastrids. *Occasional Pap. of Bernice P. Bishop Mus.* **10**, 1–27, pls 1, 2.
54. Chiba S. 1998 Synchronized evolution in lineages of land snails in oceanic islands. *Paleobiology* **24**, 99–108. (doi:10.1017/s0094837300019990)

55. Cook LM, Goodfriend GA, Cameron RAD. 1993 Changes in the land snail fauna of eastern Madeira during the Quaternary. *Phil. Trans. R. Soc. Lond. B* **339**, 83–103. (doi:10.1098/rstb.1993.0006)
56. Cameron RAD, Cook LM, Goodfriend GA, Seddon MB. 2006 Fossil land snail faunas of Porto Santo, Madeiran Archipelago: change and stasis in Pleistocene to Recent times. *Malacologia* **49**, 25–59. (doi:10.4002/1543-8120-49.1.25)
57. Goodfriend GA, Mitterer RM. 1988 Late Quaternary land snails from the north coast of Jamaica: local extinctions and climatic change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63**, 293–311. (doi:10.1016/0031-0182(88)90101-0)
58. Riedel A, Norris A. 1987 An undescribed species of *Zonites* from the island of Santorini, Greece. *J. Conchol.* **32**, 377–378. (doi:10.5962/p.407915)
59. Liberto F, Grano M, Cattaneo C, Gregorini A, Colomba M. 2024 New data on land and freshwater molluscs of Sifnos Island and Kitriani Islet (Cyclades, Greece). *Zool. Anz.* **313**, 130–148. (doi:10.1016/j.jcz.2024.08.010)
60. Coppo G. 2000 Invertebrate research overview: 2. The endemic land snails. *Bull. De L'Institut R. Des Sci. Nat. De Belg.* **70** Supplement, 27–29.
61. Mourer-Chauviré C, Bour R, Ribes S, Moutou F. 1999 The avifauna of Réunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. *Smithson. Contrib. Paleobiology* **89**, 1–38.
62. Smith BJ, Djajasmita M. 1988 The land molluscs of the Krakatau Islands, Indonesia. *Phil. Trans. R. Soc. Lond. B* **323**, 379–400. (doi:10.1098/rstb.1988.0133)
63. Paulay G. 1994 Biodiversity on oceanic islands: its origin and extinction. *Am. Zool.* **34**, 134–144. (doi:10.1093/icb/34.1.134)
64. Cowie RH. 2022 Evolution, extinction and conservation of native Pacific island land snails. In *Imperiled: the encyclopedia of conservation* (eds DA DellaSala, MI Goldstein), pp. 395–404, vol. 1. Elsevier. (doi:10.1016/b978-0-12-821139-7.00023-4)
65. Ladefoged TN, Kirch PV, Gon SM III, Chadwick OA, Hartshorn AS, Vitousek PM. 2009 Opportunities and constraints for intensive agriculture in the Hawaiian archipelago prior to European contact. *J. Archaeol. Sci.* **36**, 2374–2383. (doi:10.1016/j.jas.2009.06.030)
66. Kagawa-Viviani AK, Lincoln NK, Quintus S, Lucas MP, Giambelluca TW. 2018 Spatial patterns of seasonal crop production suggest coordination within and across dryland agricultural systems of Hawai'i Island. *Ecol. Soc.* **23**, 20. (doi:10.5751/es-10369-230320)
67. Christensen CC, Kirch PV. 1986 Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. *Bish. Mus. Occas. Pap.* **26**, 52–80.
68. Shiels AB, Flores CA, Khamsing A, Krushelnicky PD, Mosher SM, Drake DR. 2013 Dietary niche differentiation among three species of invasive rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*). *Biol. Invasions* **15**, 1037–1048. (doi:10.1007/s10530-012-0348-0)
69. Cox G. 1999 *Alien species in North America and Hawaii: impacts on natural ecosystems*. Washington, DC: Island Press.
70. Hadfield MG. 1986 Extinction in Hawaiian achatinelline tree snails. *Malacologia* **27**, 67–81.
71. Fischer JR. 2007 Cattle in Hawai'i: biological and cultural exchange. *Pac. Hist. Rev.* **76**, 347–372. (doi:10.1525/phr.2007.76.3.347)
72. Wehr NH, Hess SC, Litton CM. 2018 Biology and impacts of Pacific islands invasive species. 14. *Sus scrofa*, the feral pig (Artiodactyla: Suidae). *Pac. Sci.* **72**, 177–198. (doi:10.2984/72.2.1)
73. Chynoweth M, Lepczyk CA, Litton CM. 2010 Feral goats in the Hawaiian Islands: understanding the behavioral ecology of nonnative ungulates with GPS and remote sensing technology. In *Proc. of the 24th vertebrate pest conference* (eds RM Timm, KA Fagerstone), pp. 41–45. Davis, CA: University of California.
74. Chynoweth MW, Litton CM, Lepczyk CA, Hess SC, Cordell S. 2013 Biology and impacts of Pacific island invasive species. 9. *Capra hircus*, the feral goat (Mammalia: Bovidae). *Pac. Sci.* **67**, 141–156. (doi:10.2984/67.2.1)
75. Hess SC, Van Vuren DH, Witmer GW. 2017 Feral goats and sheep. In *Ecology and management of terrestrial vertebrate invasive species in the United States* (eds WC Pitt, JC Beasley, GW Witmer), pp. 289–309. Boca Raton, FL: CRC Press. (doi:10.1201/9781315157078-14)
76. Bartholomew DP, Hawkins RA, Lopez JA. 2012 Hawaii pineapple: the rise and fall of an industry. *HortScience* **47**, 1390–1398. (doi:10.21273/HORTSCI.47.10.1390)
77. Perroy RL, Melrose J, Cares S. 2016 The evolving agricultural landscape of post-plantation Hawai'i. *Appl. Geogr.* **76**, 154–162. (doi:10.1016/j.apgeog.2016.09.018)
78. Maly K, Wilcox BA. 2000 A short history of cattle and range management in Hawaii. *Rangelands* **22**, 21–23. (doi:10.2458/azu_rangelands_v22i5_maly)
79. Hadway LJ, Hadfield MG. 1999 Conservation status of tree snail species in the genus *Partulina* (Achatinellinae) on the island of Hawai'i: a modern and historical perspective. *Pac. Sci.* **53**, 1–14.
80. Ellsworth LM, Litton CM, Dale AP, Miura T. 2014 Invasive grasses change landscape structure and fire behaviour in Hawaii. *Appl. Veg. Sci.* **17**, 680–689. (doi:10.1111/avsc.12110)
81. Motley TJ, Luongo A, Meyer J-Y. 2014 Vegetation types and map of Rapa. In *Terrestrial biodiversity of the Austral Islands, French Polynesia* (eds J-Y Meyer, EM Claridge), pp. 133–147. Paris, France: Muséum national d'Histoire naturelle.
82. Cooke CM Jr. 1935 Report of C. Montague Cooke, Jr. *Bish. Mus. Bull.* **133**, 36–56.
83. Brook FJ. 2010 Coastal landsnail fauna of Rarotonga, Cook Islands: systematics, diversity, biogeography, faunal history, and environmental influences. *Tuhinga* **21**, 161–252. (doi:10.3897/tuhinga.21.e34189)
84. Abdou A, Bouchet P. 2000 Nouveaux gastéropodes Endodontidae et Punctidae (Mollusca, Pulmonata) récemment éteints de l'archipel des Gambier (Polynésie). *Zoosystema* **22**, 689–707.
85. Bouchet P, Abdou A. 2001 Recent extinct land snails (Euconulidae) from the Gambier Islands with remarkable apertural barriers. *Pac. Sci.* **55**, 121–127. (doi:10.1353/psc.2001.0011)
86. Bouchet P, Abdou A. 2003 Endemic land snails from the Pacific Islands and the museum record: documenting and dating the extinction of the terrestrial Assimineidae of the Gambier Islands. *J. Molluscan Stud.* **69**, 165–170. (doi:10.1093/mollus/69.3.165)
87. Preece RC. 1998 Impact of early Polynesian occupation on the land snail fauna of Henderson Island, Pitcairn group (South Pacific). *Phil. Trans. R. Soc. B Lond. B* **353**, 347–368. (doi:10.1098/rstb.1998.0214)
88. Neubert E, Chérel-Mora C, Bouchet P. 2009 Polytypy, clines, and fragmentation: the bulimes of New Caledonia revisited (Pulmonata, Orthalicoidae, Placostylidae). *Mém. Du Muséum Natl. D'Histoire Nat.* **198**, 37–131.
89. Whitmore N, Arihafa A, Takendu W, Lamarin J. 2020 *Papustyla pulcherrima* (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2020: e.T16033A176841328. ()
90. Cowie RH. 2001 Invertebrate invasions on Pacific islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biol. Invasions* **3**, 119–136. (doi:10.1023/A:1014529019000)
91. Brook FJ, Walter RK, Craig JA. 2010 Changes in the terrestrial molluscan fauna of Miti'āro, southern Cook Islands. *Tuhinga* **21**, 75–98. (doi:10.3897/tuhinga.21.e34184)
92. Civeyrel L, Simberloff D. 1996 A tale of two snails: is the cure worse than the disease? *Biodivers. Conserv.* **5**, 1231–1252. (doi:10.1007/bf00051574)
93. Cowie RH. 2001 Can snails ever be effective and safe biocontrol agents? *Int. J. Pest Manag.* **47**, 23–40. (doi:10.1080/09670870150215577)

94. Meyer WM III, Cowie RH. 2025 Biology and impacts of Pacific island invasive species. 17. *Lissachatina fulica*, the giant African snail (Mollusca: Achatinidae; Achatininae). *Pac. Sci.* **79**, 1–35. (doi:10.2984/79.1.1)
95. Meyer WM III, Yeung NW, Slapcinsky J, Hayes KA. 2017 Two for one: inadvertent introduction of *Euglandina* species during failed bio-control efforts in Hawaii. *Biol. Invasions* **19**, 1399–1405. (doi:10.1007/s10530-016-1354-4)
96. Reyes-Tur B, Chen Z, Gordillo-Pérez MJ, Ben Hamadou A, Gerheim C, Greve C, Sigwart JD. 2025 Draft genome of the Cuban painted landsnail *Polymita picta*, International Mollusc of the Year 2022. *BMC Genom. Data* **26**, 63. (doi:10.1186/s12863-025-01356-9)
97. González-Guillén A, Berschauer DP, Pérez-Rivero R, Méndez-Hernández A. 2021 The never spoken poignant connection between Cuban tree snails and carpentry/crafts/art: the case of *Polymita* and *Liguus*. *Festivus* **53**, 128–139. (doi:10.54173/f532128)
98. Rosenberg G, Muratov IV. 2005 Status report on the terrestrial Mollusca of Jamaica. *Proc. Acad. Nat. Sci. Phila.* **155**, 117–161. (doi:10.1635/i0097-3157-155-1-117.1)
99. Goodfriend GA, Cameron RAD, Cook LM. 1994 Fossil evidence of recent human impact on the land snail fauna of Madeira. *J. Biogeogr.* **21**, 309–320. (doi:10.2307/2845532)
100. Rando JC, Pieper H, Alcover JA. 2014 Radiocarbon evidence for the presence of mice on Madeira Island (North Atlantic) one millennium ago. *Proc. R. Soc. B* **281**, 20133126. (doi:10.1098/rspb.2013.3126)
101. Lambdon P, Cronk Q. 2020 Extinction dynamics under extreme conservation threat: the flora of St Helena. *Front. Ecol. Evol.* **8**, 41. (doi:10.3389/fevo.2020.00041)
102. Smith EA. 1892 On the land-shells of St. Helena. *Proc. Zool. Soc. Lond.* 258–270.
103. Mollusc Specialist Group. 1996 *Succinea sanctaehelenae*. The IUCN Red List of Threatened Species 1996: e.T21132A9249529. (doi:10.2305/IUCN.UK.1996.RLTS.T21132A9249529.en)
104. White L, Pryce D. 2014 *Helenoconcha relicta*. The IUCN Red List of Threatened Species 2014: e.T9764A64399435. (doi:10.2305/IUCN.UK.2014-3.RLTS.T9764A64399435.en)
105. Panisi M. 2023 Ex-situ efforts for the conservation of the endangered Obô giant snail *Archachatina bicarinata* in the Gulf of Guinea, Central Africa. *Tentacle* **31**, 47–49.
106. Griffiths O, Herbert DG. 2022 Gastropoda, terrestrial and freshwater Mollusca (snails), Sifotra. In *The new natural history of Madagascar* (ed. SM Goodman), pp. 860–872, vol. 1. Princeton, NJ and Woodstock, NY: Princeton University Press. (doi:10.2307/j.ctv2ks6tbb.111)
107. Muratov IV, Abdou A, Bouchet P. 2005 Charopid land snails (Gastropoda Pulmonata Charopidae) from Mayotte, Comores: alive and well. *Trop. Zool.* **18**, 171–208. (doi:10.1080/03946975.2005.10531220)
108. Ibouroi MT, Dhurham SAO, Besnard A, Lescureux N. 2021 Understanding drivers of unsustainable natural resource use in the Comoro Islands. *Trop. Conserv. Sci.* **25**, 1–21. (doi:10.1177/19400829211032585)
109. Fontaine B, Adou A, Bidault E, Hugel S, Pignal M, Rouhan G. 2012 *Connaître pour Conserver le Patrimoine Naturel Caché des Comores*. Fondation pour la Recherche sur la Biodiversité, Unpublished report.
110. Fischer-Piette E, Vukadinovic D. 1974 Les mollusques terrestres des îles Comores. *Mémoires Du Muséum National d'Histoire Naturelle, Paris (A, Zoologie)* **84**, 1–76.
111. Strasberg D, Rouget M, Richardson DM, Baret S, Dupont J, Cowling RM. 2005 An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. *Biodivers. Conserv.* **14**, 3015–3032. (doi:10.1007/s10531-004-0258-2)
112. Florens FBV, Baider C, Martin GMN, Strasberg D. 2012 Surviving 370 years of human impact: what remains of tree diversity and structure of the lowland wet forests of oceanic island Mauritius? *Biodivers. Conserv.* **21**, 2139–2167. (doi:10.1007/s10531-012-0304-4)
113. Florens FBV. 2013 Conservation in Mauritius and Rodrigues: challenges and achievements from two ecologically devastated oceanic islands. In *Conservation biology: voices from the tropics* (eds NS Sodhi, L Gibson, PH Raven), pp. 40–50. Newark, NJ: John Wiley & Sons. (doi:10.1002/9781118679838)
114. Cheke AS. 1987 An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. In *Studies of Mascarene Island birds* (ed. AW Diamond), pp. 5–89. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511735769.003)
115. Thébaud C, Warren BH, Strasberg D. 2009 Mascarene Islands, Biology. In *Encyclopedia of islands* (eds RG Gillespie, DA Clague), pp. 612–619. Berkeley, CA, Los Angeles, CA, London, UK: University of California Press. (doi:10.1525/9780520943728-146)
116. Griffiths OL, Florens FBV. 2004 Ten new species of Mascarene land snails (Mollusca: Gastropoda) and their conservation status. *Molluscan Res.* **24**, 161–177. (doi:10.1071/MR04015)
117. Gerlach J. 1996 Patterns of hybridization and extinction in a tropical land snail. *Phelsuma* **4**, 27–38.
118. Gerlach J. 2006 *Terrestrial and freshwater Mollusca of the Seychelles Islands*. Leiden, The Netherlands: Backhuys Publishers.
119. Harper GA, Bunbury N. 2015 Invasive rats on tropical islands: their population biology and impacts on native species. *Glob. Ecol. Conserv.* **3**, 607–627. (doi:10.1016/j.gecco.2015.02.010)
120. Brook FJ. 2000 Prehistoric predation of the landsnail *Placostylus ambagiosus* Suter (Stylommatophora: Bulimulidae), and evidence for the timing of establishment of rats in northernmost New Zealand. *J. R. Soc. N. Z.* **30**, 227–241. (doi:10.1080/03014223.2000.9517619)
121. Atkinson IAE. 1977 A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pac. Sci.* **31**, 109–133.
122. Chiba S. 2010 Invasive rats alter assemblage characteristics of land snails in the Ogasawara Islands. *Biol. Conserv.* **143**, 1558–1563. (doi:10.1016/j.biocon.2010.03.040)
123. Cowie RH. 1997 Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. *Bish. Mus. Occas. Pap.* **50**, 1–66.
124. Davis CJ, Butler DG. 1964 Introduced enemies of the giant African snail, *Achatina fulica* Bowdich, in Hawaii. *Proc. Hawaii. Entomol. Soc.* **18**, 377–389.
125. Nishida T, Napompeth B. 1975 Effect of age-specific predation on age distribution and survival of the giant African snail, *Achatina fulica*. *Proc. Hawaii. Entomol. Soc.* **22**, 119–123.
126. Hadfield MG, Mountain BS. 1980 A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. *Pac. Sci.* **34**, 345–358.
127. Tillier S, Clarke BC. 1983 Lutte biologique et destruction du patrimoine génétique: le cas des mollusques gastéropodes pulmonés dans les territoires français du Pacifique. *Genet. Sel. Evol.* **15**, 559–566. (doi:10.1186/1297-9686-15-4-559)
128. Coote T, Loève É. 2003 From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. *Oryx* **37**, 91–96. (doi:10.1017/s0030605303000176)
129. Burch JB. 2007 A new species of land snail (Stylommatophora: Partulidae) from Raiatea, French Polynesia, Oceania. *Occas. Pap. Mus. Zool. Univ. Mich.* **740**, 1–8.
130. Lee T, Burch JB, Coote T, Pearce-Kelly P, Hickman C, Meyer J-Y, Ó Foighil D. 2009 Moorean tree snail survival revisited: a multi-island genealogical perspective. *BMC Evol. Biol.* **9**, 204. (doi:10.1186/1471-2148-9-204)
131. Griffiths O, Cook A, Wells SM. 1993 The diet of the introduced carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *J. Zool.* **229**, 79–89. (doi:10.1111/j.1469-7998.1993.tb02622.x)
132. Gargominy O. 2007 Pas seulement des *Partula* au menu d'*Euglandina rosea*. *MalaCo* **4**, 150–151.
133. Meyer WM III, Cowie RH. 2010 Feeding preferences of two predatory snails introduced to Hawaii and their conservation implications. *Malacologia* **53**, 135–144. (doi:10.4002/040.053.0106)

134. Cadet V, Huet N. 2025 First discovery of living *Clatripoma conoidea* (L. Pfeiffer, 1846) (Caenogastropoda: Littorinimorpha: Pomatiidae) on Reunion Island. *Folia Malacol.* **33**, 82–85. (doi:10.12657/folmal.033.005)
135. Sugiura S. 2010 Prey preference and gregarious attacks by the invasive flatworm *Platydemus manokwari*. *Biol. Invasions* **12**, 1499–1507. (doi:10.1007/s10530-009-9562-9)
136. Sugiura S. 2009 Seasonal fluctuation of invasive flatworm predation pressure on land snails: implications for the range expansion and impacts of invasive species. *Biol. Conserv.* **142**, 3013–3019. (doi:10.1016/j.biocon.2009.07.032)
137. Muniappan R, Duhamel G, Santiago RM, Acay DR. 1986 Giant African snail control in Bugsuk island, Philippines, by *Platydemus manokwari*. *Oléagineux* **41**, 183–186.
138. Kawakatsu M, Okochi K, Sato H, Okochi K, Ohbayashi T, Kitagawa K, Totani K. 1999 *A preliminary report on land planarians (Turbellaria, Seriata, Tricladida, Terricola) and land nemertine [sic] (Enopla, Hoplonemertea, Monostylifera) from the Ogasawara Islands*. Occasional Publications, Biological Laboratory of Fuji Women's College, Sapporo (Hokkaidō), Japan, pp. 1–8.
139. Muniappan R. 1990 Use of the planarian, *Platydemus manokwari*, and other natural enemies to control the giant African snail. In *The use of natural enemies to control agricultural pests* (ed. J Bay-Petersen), pp. 179–183. Taipei, Taiwan: Food and Fertilizer Technology Center for the Asian and Pacific Region.
140. Brodie G, Barker G, Haynes A, Singh R, Stevens F, Fiu M, Bogitini L, Matewai M, Naivalurua J. 2013 *Documentation of Fiji's endemic and introduced land snail Fauna. Biodiversity conservation lessons learned technical series 23*. Apia, Samoa: Conservation International.
141. Muniappan R. 1987 Biological control of the giant African snail, *Achatina fulica* Bowdich, in the Maldives. *FAO Plant Prot. Bull.* **35**, 127–133.
142. Outerbridge ME, Ovaska K, Garcia G. 2019 Back from the brink: recovery efforts for endemic land snails of Bermuda. *Tentacle* **27**, 16–18.
143. Solem A. 1976 *Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part I. Family Endodontidae*. Chicago, IL: Field Museum of Natural History. (doi:10.5962/bhl.title.2554)
144. Solem A. 1983 *Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography*. Chicago, IL: Field Museum of Natural History. (doi:10.5962/bhl.title.2553)
145. Kraus F, Medeiros A, Preston D, Jarnevič CS, Rodda GH. 2012 Diet and conservation implications of an invasive chameleon, *Chamaeleo jacksonii* (Squamata: Chamaeleonidae) in Hawaii. *Biol. Invasions* **14**, 579–593. (doi:10.1007/s10530-011-0099-3)
146. Chiaverano LM, Holland BS. 2014 Impact of an invasive predatory lizard on the endangered Hawaiian tree snail *Achatinella mustelina*: a threat assessment. *Endanger. Species Res.* **24**, 115–123. (doi:10.3354/esr00589)
147. Maroulis L, Poulakakis N, Proios K, Karakasi D, Triantis KA, Mylonas M, Vardinoyannis K. 2025 On the path to extinction: *Helix godetiana* Kobelt, 1878, the only threatened *Helix* species in Greece. *Nat. Conserv.* **58**, 1–10. (doi:10.3897/natureconservation.58.129016)
148. Cowie RH. 2005 Alien non-marine molluscs in the islands of the tropical and subtropical Pacific: a review. *Am. Malacol. Bull.* **20**, 95–103.
149. Panisi M, Sinclair R, Bird TLF, Lima RF. 2022 *Archachatina bicarinata*. The IUCN Red List of Threatened Species: e.T2039A160300790. (doi:10.2305/IUCN.UK.2022-2.RLTS.T2039A160300790.en)
150. Cowie RH, Fontaine B, Bouchet P. 2023 Non-marine Molluscs. In *The living planet – the state of the world's wildlife* (ed. N Maclean), pp. 288–310. Cambridge, UK: Cambridge University Press. (doi:10.1017/9781108758826.016)
151. Dixon G. 1789 *A voyage round the world; but more particularly to the north-west coast of America: performed in 1785, 1786, and 1788, in the King George and Queen Charlotte, Captains Portlock and Dixon*. London, UK: G. Goulding. (doi:10.5962/bhl.title.59710)
152. Sischo DR. 2020 Hawaii Snail Extinction Prevention Program (SEPP). *Tentacle* **28**, 27–29.
153. Cowie RH, Rundell RJ, Yeung NY. 2017 *Samoan land snails and slugs. an identification guide*. Pago Pago: American Samoa Government.
154. 2017 CITES. See <https://www.cites.org/eng/app/appendices.php>.
155. Zhang G, Wu M. 2020 Internet shell trade, a new threat to malacodiversity. *Tentacle* **28**, 12–14.
156. Challender DWS, Hinsley A, Milner-Gulland EJ. 2019 Inadequacies in establishing CITES trade bans. *Front. Ecol. Environ.* **17**, 199–200. (doi:10.1002/fee.2034)
157. Gerlach J. 2007 Short-term climate change and the extinction of the snail *Rhachistia aldabrae* (Gastropoda: Pulmonata). *Biol. Lett.* **3**, 581–584. (doi:10.1098/rsbl.2007.0316)
158. Battarbee RW. 2014 The rediscovery of the Aldabra banded snail, *Rhachistia aldabrae*. *Biol. Lett.* **10**, 20140771. (doi:10.1098/rsbl.2014.0771)
159. Mancina CA, Hernández M, Martínez D, Estrada R. 2017 An assessment of the potential effects of climate change on the distribution of painted land snail species, genus *Polymita* (Gastropoda: Cepolidae). *Tentacle* **25**, 17–19.
160. Pearce TA, Paustian ME. 2013 Are temperate land snails susceptible to climate change through reduced altitudinal ranges? A Pennsylvania example. *Am. Malacol. Bull.* **31**, 213–224. (doi:10.4003/006.031.0201)
161. Murphy MJ, Shea M. 2015 Survey of the land snail fauna (Gastropoda: Pulmonata) of Mount Kaputar National Park in northern inland New South Wales, Australia, including a description of the listing of Australia's first legally recognised endangered land snail community. *Molluscan Res.* **35**, 51–64. (doi:10.1080/13235818.2014.948147)
162. Murphy M, Murphy JK, Faris CJ, Mulholland MJ. 2019 Marooned on an extinct volcano: the conservation status of four endemic land snails (Gastropoda: Pulmonata) at Mount Kaputar, New South Wales. *Proc. Linn. Soc. N. S. W.* **141**, S33–S44.
163. Gargominy O. 2008 Beyond the alien invasion: a recently discovered radiation of Nesopupinae (Gastropoda: Pulmonata: Vertiginidae) from the summits of Tahiti (Society Islands, French Polynesia). *J. Conchol.* **39**, 517–536.
164. Valle S, Pereira DJ, Matthews TJ, Martin TE. 2025 Heightened extinction risk due to tropical cyclones in insular biodiversity hotspots. *Biol. Conserv.* **307**, 111184. (doi:10.1016/j.biocon.2025.111184)
165. Osborne TR, Rundell RJ. 2025 Not blown away: over three-quarters of species in a Pacific atoll land snail assemblage remain five years post-typhoon. *Am. Malacol. Bull.* **41**, 112–118. (doi:10.4003/006.040.0202)
166. Pearce-Kelly P, Mace GM, Clarke D. 1995 The release of captive bred snails (*Partula taeniata*) into a semi-natural environment. *Biodivers. Conserv.* **4**, 645–663. (doi:10.1007/bf00222520)
167. Pearce-Kelly P, Clarke D, Walker C, Atkin P. 1997 A conservation programme for the partulid tree snails of the Pacific region. *Memoirs Mus. Vic.* **56**, 431–433. (doi:10.24199/j.mmv.1997.56.34)
168. Clarke D. 2019 *EAZA Best Practice Guidelines for Polynesian tree snails (Partula spp)*, 1st edn. Amsterdam, The Netherlands: European Association of Zoos and Aquariums.
169. Pearce-Kelly P. 2022 *Partula* conservation programme update. *Tentacle* **30**, 40.
170. Richardson K, Prince H, Kelton K, Lambert K, Papp T, Garcia G. 2023 Preventing extinction: the past decade of snail conservation at Chester Zoo. *Tentacle* **31**, 41–44.
171. Pearce-Kelly P, Gerlach J. 2023 *Partula* conservation programme update. *Tentacle* **31**, 50–51.
172. Gerlach J, Pearce-Kelly P. 2025 *Partula* 2024: reintroduction bears fruit at last. *Tentacle* **33**, 41–43.
173. Gerlach J, Pearce-Kelly P. 2024 A momentous year for *Partula* conservation. *Tentacle* **32**, 32–34.

174. Coote T, Clarke D, Hickman CS, Murray J, Pearce-Kelly P. 2004 Experimental release of endemic *Partula* species, extinct in the wild, into a protected area of natural habitat on Moorea. *Pac. Sci.* **58**, 429–434. (doi:10.1353/psc.2004.0028)
175. Coote T *et al.* 2017 Ten endemic species of *Partula* reintroduced onto three of the Society Islands. *Tentacle* **25**, 36–38.
176. Hadfield MG, Holland BS, Olival KJ. 2004 Contributions of ex situ propagation and molecular genetics to conservation of Hawaiian tree snails. In *Experimental approaches to conservation biology* (eds MS Gordon, SM Bartol), pp. 16–34. Berkeley, CA, Los Angeles, CA, London, UK: University of California Press. (doi:10.1525/california/9780520240247.003.0003)
177. Sischo DR. 2016 Introduction to the Hawaii Snail Extinction Prevention Program (SEPP). *Tentacle* **24**, 49–51.
178. Olival KJ, Hadfield MG. 2000 Hawaiian *Achatinella/Partulina* tree snail update. *Tentacle* **9**, 12.
179. Sischo DR. 2025 Hawaii Snail Extinction Prevention Program (SEPP). *Tentacle* **33**, 47–48.
180. Hayes KA, Derne B, Earl C, Kealoha J, Yeung NW. 2022 Hawaiian land snail conservation updates. *Tentacle* **30**, 41–44.
181. Sischo DR. 2022 Hawaii Snail Extinction Prevention Program (SEPP). *Tentacle* **30**, 44–46.
182. Sischo DR. 2024 Hawaii Snail Extinction Prevention Program (SEPP). *Tentacle* **32**, 37–39.
183. Chiba S. 2003 Extinction and conservation of the endemic land snails of the Ogasawara Islands. *Tentacle* **11**, 13–14.
184. Mori H, Inada M, Chiba S. 2020 Conservation programmes for endemic land snails in the Ogasawara Islands: captive breeding and control of invasive species. *Tentacle* **28**, 23–27.
185. Mori H, Inada M, Chiba S. 2021 Translocation of endangered *Mandarina* in the Ogasawara Islands. *Tentacle* **29**, 36–37.
186. Mori H, Inada M, Waki T, Chiba S. 2024 Progress in translocation of *Mandarina* snails in the Ogasawara Islands. *Tentacle* **32**, 35–37.
187. Shoji K, Wada S, Chiba S. 2025 Captive breeding of endangered cloud forest land snails from Ogasawara. *Tentacle* **33**, 43–45.
188. Outerbridge ME, Ovaska K, Garcia G. 2021 Recovery efforts for endemic Bermuda land snails continue. *Tentacle* **29**, 9–12.
189. Teixeira D, Garcia G, Bushell M, de Zoeten T. 2023 Rescuing four critically endangered land snails from extinction (Desertas Islands: Portugal). *Tentacle* **31**, 51–53.
190. Richardson K, Teixeira D, Papp T, Prince H, Kelton K, Newens-Hill I, Redbond J, Garcia G. 2025 Progress and insights from the Desertas Islands ex-situ snail conservation programme. *Tentacle* **33**, 45–46.
191. Griffiths C, Zuñel N. 2023 The return of *Pachystyla bicolor*. *Tentacle* **31**, 49–50.
192. Fernandes DM *et al.* 2021 A genetic history of the pre-contact Caribbean. *Nature* **590**, 103–110. (doi:10.1038/s41586-020-03053-2)
193. Schrader J *et al.* 2024 Islands are key for protecting the world's plant endemism. *Nature* **634**, 868–874. (doi:10.1038/s41586-024-08036-1)
194. Briggs JC. 2017 Emergence of a sixth mass extinction? *Biol. J. Linn. Soc.* **122**, 243–248. (doi:10.1093/biolinnean/blx063)
195. Wiens JJ, Saban KE. 2025 Questioning the sixth mass extinction. *Trends Ecol. Evol.* **40**, 375–384. (doi:10.1016/j.tree.2025.01.002)
196. Wiens JJ, Saban KE. 2025 Proponents of the sixth mass extinction admit it is unsupported. *Trends Ecol. Evol.* **40**, 724–725. (doi:10.1016/j.tree.2025.06.012)